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BRIEF COMMUNICATION

Evolutionary Roots of Motor Planning: The End-State Comfort Effect in Lemurs

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Humans (*Homo sapiens*) anticipate the consequences of their forthcoming actions. For example, they grasp objects with uncomfortable grasps to afford comfortable end positions—the end-state comfort (ESC) effect. When did such sophisticated motor planning abilities emerge in evolution? We addressed this question by asking whether humans' most distant living primate relatives—lemurs—also exhibit the ESC effect. We presented 6 species of lemurs (*Lemur catta*, *Eulemur mongoz*, *Eulemur coronatus*, *Eulemur collaris*, *Hapalemur griseus*, and *Varecia rubra*) with a food extraction task and measured the grasp used—either a canonical thumb-up posture or a noncanonical thumb-down posture. The lemurs adopted the thumb-down posture when that hand position afforded a thumb-up posture following object transport, thereby exhibiting the ESC effect. We conclude that the planning abilities underlying the ESC effect evolved at least 65 million years ago, or 25 million years earlier than previously supposed based on an earlier demonstration of the ESC effect in cotton-top tamarins (*Saguinus oedipus*; Weiss, Wark, & Rosenbaum, 2007). Because neither cotton-tops nor lemurs are tool users, the data suggest that the cognitive abilities implicated by the ESC effect are not sufficient, although they may be necessary, for tool use.

Keywords: motor planning, lemur, prosimian

Planning to grasp an object involves more complex processing than one might assume. Even a seemingly simple behavior like picking up a ball involves the selection of a particular sequence of movements from an infinite set of possibilities. Constraints limit the types of behaviors that are performed, however. One such constraint relates to what the actor intends to do with the object. Research with human adults has shown that when people grasp objects, they not only consider the physical affordances of the objects in their current state; they also consider the future demands of the transfer to be achieved. Actors usually organize their grasping behaviors to accommodate future postures that afford greatest comfort at the termination of the transfer maneuver (Rosenbaum et al., 1990). This effect, called the *end-state comfort effect* (hereafter the ESC effect), has been documented in a number of laboratory tasks (see Rosenbaum, Cohen, Meulenbroek, & Vaughan, 2006). Psychophysical ratings of comfort and discomfort confirm that people are willing to adopt uncomfortable postures in the service of later, more comfortable postures when grasping objects to be moved from one position to another.

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Given the cognitive prerequisites of such anticipatory planning (see Rosenbaum, 2010), researchers have taken an interest in the ontogenetic and phylogenetic roots of this ability. On the ontogenetic front, Claxton, Keen, and McCarty (2003) showed that 10-month-old infants reach more quickly for a ball when the subsequent action requires less precision (e.g., throwing) than when the subsequent action requires greater precision (e.g., fitting the ball into a tube). McCarty, Clifton, and Collard (1999, 2001) showed that these rudimentary anticipatory planning skills become more refined with age. For example, in a series of studies investigating how infants grasped a spoon, these researchers found that whereas 9- to 12-month-old infants did not evidence task-appropriate hand orientations, 19- to 24-month-old infants did.

Continuing on the ontogenetic front, a surprising result has also been obtained. Despite the seemingly precocious emergence of the planning abilities just described, the ESC effect appears not to be in place until well past 6 years of age. Adalbjornsson, Fischman, and Rudisill (2008) found that 5- to 6-year-old children do not invert their hands to turn over a cup and fill it with water, in contrast to what is seen in young adults (Fischman, 1997). Weigelt and Schack (in press) obtained similar results. Stoeckel, Weigelt, Beeger, and Schack (2009) found that only by around 9 years of age is the ESC effect manifested at a statistical rate comparable to that seen in young adults. In sum, anticipatory abilities appear early in ontogeny but exhibit a protracted developmental trajectory en route to adult proficiency.

Whereas a number of studies have explored the *ontogenetic* roots of anticipatory motor planning, much less research has been devoted to the *phylogenetic* roots of these anticipatory abilities.

This is surprising given that physical anthropologists have long placed great emphasis on the structure of the hand and its presumed capabilities for grasping (e.g., Bloch & Boyer, 2002), and given as well that neurophysiologists have examined reaching behaviors in monkeys, including qualitative evaluations of grasping postures deployed for objects of various size (e.g., Rizzolatti et al., 1988). To date, however, only one study that we know of has documented whether anticipatory motor planning is manifested in nonhuman grasping. Weiss et al. (2007) showed that cotton-top tamarins, which are non–tool-using New World monkeys, exhibit the ESC effect. Weiss et al. used a task that required inversion of a plastic cup for food extraction. The tamarins inverted their grasping posture to accommodate the future task demand. This outcome suggests that anticipatory motor planning has a lengthy evolutionary history. On the other hand, the result casts doubt on the view that the abilities indexed by the ESC effect are sufficient for tool use (Johnson-Frey, 2004). If the ability to plan well enough to exhibit the ESC effect was sufficient for tool use, one would expect to see cotton-top tamarins using tools in the wild and in captivity. However, the available evidence does not support this view (e.g., Santos, Rosati, Sproul, Spaulding, & Hauser, 2005).

The present study was designed to extend the previous work on cotton-top tamarins by asking whether primates that are even more distantly related to humans—namely, lemurs—also exhibit the ESC effect. Lemurs are prosimian primates. They are the most evolutionarily distant primate relatives of *Homo sapiens* (Yoder, 2007), having diverged from hominids roughly 20 million years before New World monkeys did. We were interested in whether lemurs exhibit the ESC effect, not just so we could determine whether this and related motor planning abilities characterize this distantly related primate species, but also to see how early in evolution such abilities may have emerged.

In terms of what could be expected of lemurs in our task, the literature sends mixed messages. Early reports suggested that lemurs lack many of the cognitive abilities found in simian primates (Jolly, 1966). More contemporary studies have reported that there are a number of cognitive domains in which lemurs perform similarly to monkeys (e.g., Lewis, Jaffe, & Brannon, 2005; Santos, Mahajan, & Barnes, 2005). However, lemurs may have poor planning abilities relative to monkeys, as indexed by their limited foraging skills (Cunningham & Janson, 2007) and as suggested by their brain differences from simians (Kaas, 2004). Furthermore, there are marked morphological differences that may constrain lemurs' motor planning abilities. Unlike simian primates, lemurs have only one hand posture for holding objects (the power grip), and they show a lack of manual dexterity and flexibility for hand positions (Bishop, 1962). In general, lemurs often manipulate objects with their mouths instead of their hands (Jolly, 1964). On the basis of these considerations, we thought it was not a foregone conclusion that lemurs would exhibit the ESC effect.

Method

Subjects

Nine male and five female lemurs of six species were included. The species and sexes of the subjects were as follows (males: females): ring-tailed lemur (*Lemur catta*) 2:0; mongoose lemur (*Eulemur mongoz*) 4:2; crowned lemur (*Eulemur coronatus*) 1:1; collared lemur (*Eulemur collaris*) 1:0; eastern lesser bamboo lemur (*Hapalemur griseus*) 1:1; red ruffed lemur (*Varecia rubra*) 0:1. All 14 subjects were mature adults with the exception of one infant, a 4-month-old female red ruffed lemur. Lemurs were removed from analysis if they did not grasp the stem 3 times during the inverted test condition. Six additional lemurs did not meet this criterion, and thus were not included in the analysis.

The lemurs lived at the Lemur Conservation Foundation's Myakka City Lemur Reserve. Lemurs were housed in mated pairs or small troops in indoor–outdoor habitats. Use and care of the lemur colony conformed to rules and regulations of the IACUC at the Lemur Conservation Foundation as well as at The Pennsylvania State University.

Stimuli and Apparatus

Experiments were conducted in the indoor or outdoor rooms at the Lemur Reserve. All trials were recorded with a digital camcorder. In each trial, subjects had the opportunity to remove and eat a raisin stuck to the bottom of a plastic champagne cup (Wilton Enterprises, Westport, CT). The cup was 1 in. deep and had an elongated .25 in. wide stem. The opening was 2 in. in diameter. Two stem lengths were used to accommodate lemurs of different sizes (2.25 in. and 4.25 in.). For each trial, half-pieces of raisin were stuck to the bottom of the cup.

Procedure

Most lemurs were familiarized with the task in three stages prior to the official test trials.[1] Such familiarization was useful given the lemurs' limited prior experience with extracting food from transparent containers. The lemurs received between two and five familiarization trials for each stage primarily on the basis of their accessibility and their success at extracting the food; the average number of familiarization trials was six. In all the familiarization stages, the lemurs could extract the food from the cup in any manner they chose.

During the first familiarization phase, the experimenter inserted a raisin into the cup while the lemur watched. The experimenter then held the cup containing the raisin with the opening facing the lemur. If the lemur grasped the cup with his or her hands (either by the bowl or the stem), the experimenter let go of the cup and allowed the lemur to extract the food inside. In the second phase of familiarization, the baited cup was placed on a flat surface with the cup opening facing the lemur. There were no constraints on how the lemur could extract the raisin. In the third phase of familiarization, the baited cup lay on the same flat surface with the cup opening facing 180 degrees away from the lemur's current position as judged by the experimenter prior to placement.

Following the familiarization phases, the lemurs participated in two test conditions, each consisting of three trials, with the start position of the lemurs the same as in the familiarization phases. In the inverted-cup condition, the baited cup was presented in an inverted fashion on a flat surface with the cup's opening facing down. In the upright-cup condition, the baited cup stood upright,

[1] Four lemurs did not receive all three stages because of the limited accessibility of these animals. However, the number of familiarization trials did not correlate with performance.

with the bowl opening pointing up at an angle of about 45 degrees, leaning against a wall or corner for support. To encourage stem use and prevent direct reaches to the bowl, the experimenter used the front of her hand to block access to the bowl if a lemur persisted in using nonstem maneuvers to manipulate the cup. This method was used for three of the lemurs in upright trials owing to those lemurs' repeated attempts to directly access the bowl's contents using the mouth and hands.[2] In the inverted-cup condition, this type of manipulation never was necessary.

In both testing conditions, the lemurs could obtain the food in any manner they pleased, but analysis of the videotaped performances was restricted to cases in which the lemurs grasped the stem. For each lemur, the first three stem-use test trials were coded for hand grasp on the stem in terms of whether the grasp was upright (thumb-up) or inverted (thumb-down). A lemur's performance on a trial was coded as conforming to the ESC effect if the lemur used an inverted grasp for the inverted cup and an upright grasp for the upright cup. This coding was based on the fact that each of these grasps given the cup's initial orientation would result in a canonical, thumb-up posture during raisin extraction (see Weiss et al., 2007).

Results

An example of an inverted grasp is shown in Figure 1. As far as the numbers are concerned, all 14 lemurs participated in the inverted-cup condition, whereas 13 of the lemurs participated in the upright-cup condition. In all of the 38 upright-cup trials, all of the 13 lemurs used upright grasps, whereas none of them used inverted grasps in this condition. In the inverted-cup condition, the 14 lemurs used inverted grasps in 16 of the 42 trials. Ten of these individuals spontaneously inverted their hand on at least one of three trials in the inverted-cup condition. The difference in the number of lemurs using an inverted grasp on at least one trial in the inverted-cup condition ($n = 10$) and in the upright-cup condition ($n = 0$) was significant ($p < .005$, paired sign test).

We examined the frequency of inverted grasps across inverted-cup test trials to determine whether lemurs learned to invert their hand as the session continued. Inverted grasps were distributed across trial number (first to third stem-use trial) in a way that did not support the learning hypothesis. The inverted grasps occurred in 37.5%, 18.8%, and 43.8% of Trials 1, 2, and 3, respectively.

Figure 1. A ring-tailed lemur (*L. catta*) using the inverted-hand posture.

With respect to species differences, lemurs belonging to five of the six tested species displayed hand inversions in the inverted-cup condition. Given the limited number of individuals tested from each species, we cannot infer that the one species that failed to show evidence of the ESC effect (crowned lemurs) would never show the effect.

Discussion

Our data show that lemurs display the ESC effect. Whereas in the upright-cup condition, all the individuals in our sample consistently deployed canonical, thumb-up grasping postures; in the inverted-cup condition, the majority of lemurs (71.4% of our sample) inverted their hands on at least one of three inverted-cup trials. The lemurs in our sample did not *always* show the ESC effect, but neither do cotton-top tamarins (Weiss et al., 2007) or humans (Rosenbaum et al., 2006). Obtaining evidence for the ESC effect in lemurs is remarkable because inverted-grasp postures have not been reported before for these prosimians, at least as far as we know. The result is also surprising given the morphological, cognitive, and neural differences between these species and others of relevance here, as mentioned earlier in this report.

The hand inversions observed in this experiment occurred on all three inverted-cup test trials and occurred with almost equal rates on the first and third trials. This result suggests that the lemurs did not learn to invert their hands over the course of the three-trial test session.

One concern about our data is that the overall percentage of inverted grasps was less than that observed before in tamarins (Weiss et al., 2007). It is possible, of course, that the two groups of animals simply differ in their overall propensity for the ESC effect, but this conclusion may be premature considering the different methodologies used in the present study and in the study of Weiss et al. (2007). Weiss et al. carried out their study in more controlled laboratory conditions than we did here. In particular, Weiss et al. used an apparatus in which a cup was secured to a frame that precluded the cotton-tops from grasping any part of the cup except for the stem. Weiss et al. also used a more extensive set of familiarization conditions and a different criterion for passing familiarization. In the present study, we used more naturalistic test conditions, as necessitated by the conservation efforts at the Lemur Reserve. Nevertheless, given our principal aim of seeing whether the ESC effect exists in lemurs, what we find most striking is that all but one of the lemur species we studied exhibited the ESC effect. Even the 4-month-old infant lemur showed the ESC effect, making our results the first we know of to demonstrate the ESC effect in a still-developing, nonhuman animal. The infant's performance was comparable to the adults; she inverted her hand on two of three stem-use trials. It is interesting, however, that she appeared clumsier than the adults, exhibiting slower and less

[2] The red ruffed infant had only two upright trials because of difficulty manipulating the stem. For these trials, the experimenter held the cup upright by the bowl.

precise hand movements than the adult lemurs. This suggests that anticipatory motor planning can precede the development of adult-like manual dexterity.

Future work will, of course, be needed to determine the precise timeline for the development of this behavior. Given the faster overall maturation of lemurs compared to humans, as well as the brachiating experiences that are available to lemurs but not to humans, it is impossible to comment yet on why the developmental trajectory for this behavior may be quicker in lemurs than in humans. It is also possible that the underlying cognitive representations for the ESC effect may differ across species (e.g., in the scope of planning).

Overall, our finding of the ESC effect in our most evolutionary remote primate relative suggests that humankind's impressive motor planning ability may have a lengthy evolutionary history and may be ubiquitous among living primates and quite possibly mammals in general. Our results suggest that the cognitive abilities indexed by the ESC effect appear to have evolved 25 million years earlier than previously thought and were likely characteristic of the ancestral primate species.

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